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THE CHROMOSOMES OF BOLIVIAN DIDELPHID MARSUPIALS

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Marsupials of the family Didelphidae (opossums and mouse opossums) comprise the most diverse metatherian group in America, with 63 species grouped in 15 genera (Gardner, 1993). Didelphid taxonomic diversity is paralleled with a corresponding wide range in latitudinal and altitudinal distribution. The family ranges from southern Canada (*Didelphis*; Nowak, 1991), southward into the Argentinean Patagonia (*Lestodelphys*; Redford and Eisenberg, 1992). Altitudinally, opossums range from the lowlands of the Amazon Basin (e.g., *Chironectes*, *Micoureus*; Emmons and Feer, 1990) to elevations as high as 3500 m (e.g., *T. pallidior*). Whereas the majority of the species of Didelphidae occur in tropical and subtropical areas of South America, they inhabit a wide range of habitats. The geographic position of Bolivia in the southern continent encompasses most of these habitats: from lowland rainforests and tropical savannahs, to dry Chacoean thorn scrub, and high elevational Puna grassland. Consequently, the majority of didelphid marsupial genera are represented in Bolivia.

The vast ecological diversity displayed by didelphid marsupials, contrasts with their chromosomal conservatism. Chromosome numbers across the Marsupialia range from 2n = 10 (*Wallabia bicolor*:

Macropodidae), to 2n = 32 (*Aepyprymnus rufescens*: Potoroidae). The distribution of chromosome numbers appears bimodal with one mode at 2n = 14, and the other 2n = 20 or 22, although the greatest number of species have the former condition. This pattern is characteristic of the family Didelphidae, as well as some Australasian families (i.e., Dasyuridae, Myrmecobiidae; Hayman *et al.*, 1987; Hayman, 1990). A 2n = 18 cytotype is also found in didelphoid marsupials (*Monodelphis*), which has been interpreted as "intermediate" in the chromosomal evolution of South American opossums (Reig *et al.*, 1977; Hayman, 1990). Associated with the lower number of chromosomes, marsupials also depict a constancy regarding the morphology of chromosomes, as reflected by the similar morphologic patterns in the karyotypes of mouse opossums (e.g., *Marmosa sensu lato*), short tailed-opossums (*Monodelphis*), and large-sized opossums of the genera *Didelphis*, *Chironectes* and *Lutreolina* (Reig *et al.*, 1977). Despite the broad distribution of didelphid marsupials in Bolivia, chromosomal data have not been published for any species. In this paper we document the karyotypes of the majority of didelphid marsupial genera that inhabit Bolivia, with comments on their karyotypic uniformity, in light of their distribution. Chromosomal data from Bolivian specimens are compared to those of the same species from other countries when these data were available in the literature. The karyotypes of *Monodelphis kunsi*, *Micoureus constantiae*, *Marmosops dorothea*, *M. noctivagus*, and *M. parvidens* are being reported for the first time. Taxonomic convention for mouse opossum follows Reig *et al.* (1987), Gardner and Creighton (1989), and Hershkovitz (1992).

MATERIALS AND METHODS

Karyotypes were obtained from bone marrow following the conventional Velban technique described by Anderson *et al.* (1987). A minimum of 10 metaphase spreads were counted for each specimen. Nomenclature for chromosome morphology and autosomal fundamental number (FN) follows Patton (1967). Chromosomes were arranged sequentially in order of decreasing size, with bi-armed

elements preceding single elements. Sex chromosomes correspond to the last pair in each figure.

SPECIMENS EXAMINED

Voucher specimens were deposited in the Museum of Southwestern Biology, University of New Mexico (MSB), in the American Museum of Natural History (AMNH), and in the Museo Nacional de Historia Natural, and the Museo "Noel Kempff Mercado" in Bolivia. All cell suspensions, in slides and frozen tissues, were deposited in the Division of Biological Materials of the MSB. Chromosomes, cell suspensions, and other data associated with each specimen are cross referenced directly to each voucher specimen, and stored in appropriate collections by a special field catalogue number (the NK number), used by the MSB at the University of New Mexico.

We examined 49 karyotypes in 19 species from Bolivia (localities are represented in Fig. 1):

Caluromys lanatus (2).-Pando, Isla Gargantúa, 180 m, 12°23'S, 68°35'W (NK 13953 and NK 13955, males). *Chironectes minimus* (5).-La Paz, La Reserva, 840 m, 15°44'S, 67°31'W (MSB 68329, MSB 68330, NK 25586, NK 25534, males; NK 25685, female). *Didelphis albiventris* (1).-Tarija, 61 km (by road) E of Tarija, 2100 m, 21°27'S, 64°19'W (NK 14628, male). *Didelphis marsupialis* (3).-La Paz, La Reserva, 840 m, 15°44'S, 67°31'W (MSB 68326, NK 25299, males; NK 25511, female). *Gracilinanus agilis* (2).-La Paz, Chijchijpa, 1114 m, 16°09'S, 67°45'W (NK 23095, female; NK 25278, male). *Marmosops dorothea* (1).-La Paz, Chijchijpa, 1114 m, 16°09'S, 62°45'W (MSB 68334, male). *Marmosops noctivagus* (1).-La Paz, Chijchijpa, 1114 m, 16°09'S 62°45'W (MSB 68333, female). *Marmosops parvidens* (1).-La Paz, La Reserva, 840 m, 15°44'S, 67°31'W (MSB NK 25679, female). *Metachirus nudicaudatus* (3).-La Paz, La Reserva, 840 m, 15°44'S, 67°31'W (MSB 68331, MSB 68332, NK 25677, females). *Micoureus cinereus* (3).-La Paz, La Reserva, 840 m, 15°44'S, 67°31'W (NK 25711, NK 25713, NK 25714, females). *Micoureus constantiae* (1).-Pando, La Cruz, 170 m, 11°24'S, 67°13'W (MSB 57001, male).

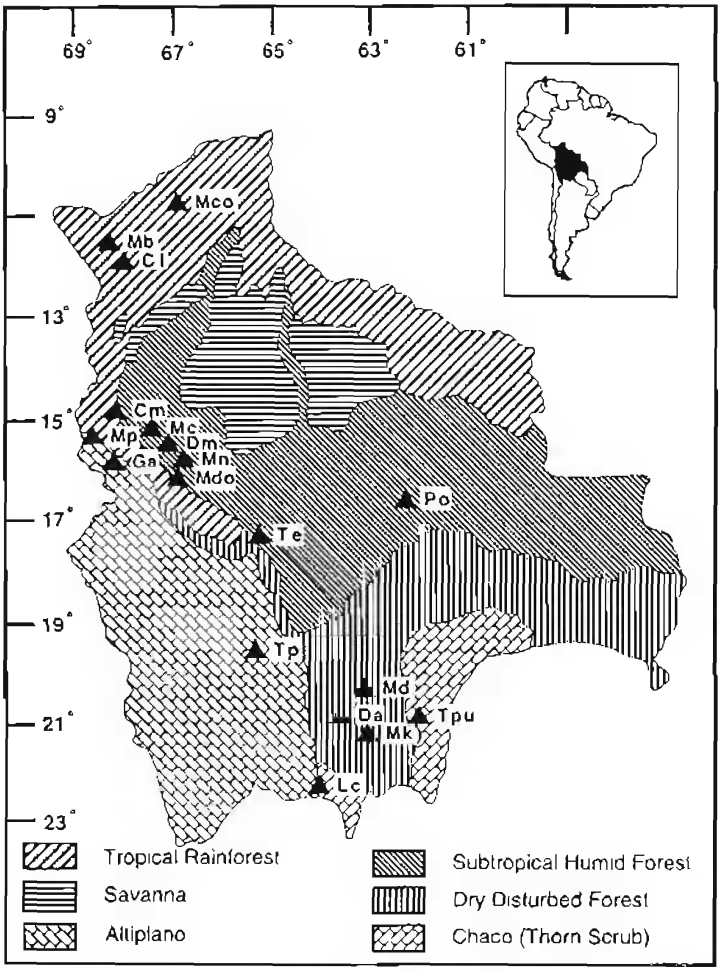

Fig. 1. Map showing the ecological zones of Bolivia (after Tosi *et al.*, 1975). Dots represent the localities of didelphid marsupials collected whose karyotypes are being reported (from north to south, and west to east): Mco = *Micoureus constantiae*; Mb = *Monodelphis brevicaudata*; Cl = *Caluromys lanatus*; Cm = *Chironectes minimus*; Mc = *Micoureus cinereus*; Mp = *Marmosops parvidens*; Dm = *Didelphis marsupialis*; Ga = *Gracilinanus agilis*; Mn = *Marmosops noctivagus*; Mdo = *Marmosops dorothea*; Po = *Philander opossum*; Te = *Thylamys elegans*; Tp = *Thylamys pallidior*; Md = *Monodelphis domestica*; Da = *Didelphis albiventris*; Tpu = *Thylamys pusillus*; Mk = *Monodelphis kunsi*; Lc = *Lutreolina crassicaudata*.

Monodelphis brevicaudata (1).-Pando, Santa Rosa, 180 m (MSB 57005, male). *Monodelphis domestica* (5).-Chuquisaca, Porvenir, 675 m, 20°45'S, 63°13'W (NK 12555, NK 12579, males; MSB 55851, NK 12668, females); Santa Cruz, Tita, 300 m, 18°25'S, 62°16'W (NK 12538, male). *Monodelphis kunsi* (1).-Tarija, Tapecua, 1500 m, 21°26'S, 63°55'W (NK 23374, female). *Philander opossum* (8).-Beni, Rio Tijamuchi, 14°56'S, 65°09'W (NK 13171, 13172, NK 13966, females); Chuquisaca, Porvenir, 675 m, 20°45'S, 63°13'W (NK 12661, female); Santa Cruz, 6 km (by road) W of Ascención (NK 13119, male; MSB 55855, NK 13118, females); 10 km N of San Ramón, 250 m, 16°36'S, 62°42'W (MSB 57007, female). *Thylamys elegans* (3).-Cochabamba, Tinkusiri, 17 km E of Totora, 2950 m, 17°45'S, 65°02'W (NK 22844, NK 23952, males); Santa Cruz, 5.5 km (by road) N of Vallegrande, 1800 m, 18°28'S, 64°08'W (NK 22986, female). *Thylamys pallidior* (4).-Chuquisaca, 68 km (by road) N of Camargo, 3400 m, 20°09'S, 65°17'W (MSB 57003, AMNH 262406, AMNH 262407, males; AMNH 262405, female). *Thylamys pusillus* (3).-Tarija, 5 km W of Estancia Bolívar, 400 m, 21°38'S, 62°37'W (NK 25140, NK 25199, males; NK 25138, female).

RESULTS

2n = 14 karyotype

The autosomal complement among *Micoureus*, *Thylamys*, and *Metachirus nudicaudatus* appear identical in terms of number and morphology with 2n = 14, and FN = 20 (Figs. 2 and 3b; Table 1). *Gracilinanus* shows a similar autosomal complement when compared with the three species of *Marmosops* (Figs. 3c-3f). These taxa have four additional submetacentric autosomal chromosomes with respect to *Thylamys* and *Micoureus* (Fig. 2). *Caluromys lanatus* (2n = 14, FN = 22) has an additional pair of biarmed (submetacentric) chromosomes if compared to *Metachirus*, *Micoureus*, and *Thylamys* (Figs. 3a and 3b). The X chromosomes of *T. pusillus*, *Gracilinanus*, *Marmosops noctivagus*, and *M. parvidens*, are submetacentrics, in contrast to the acrocentric Xs found in the other marmosines (Table 1, Figs. 2 and 3). The Y

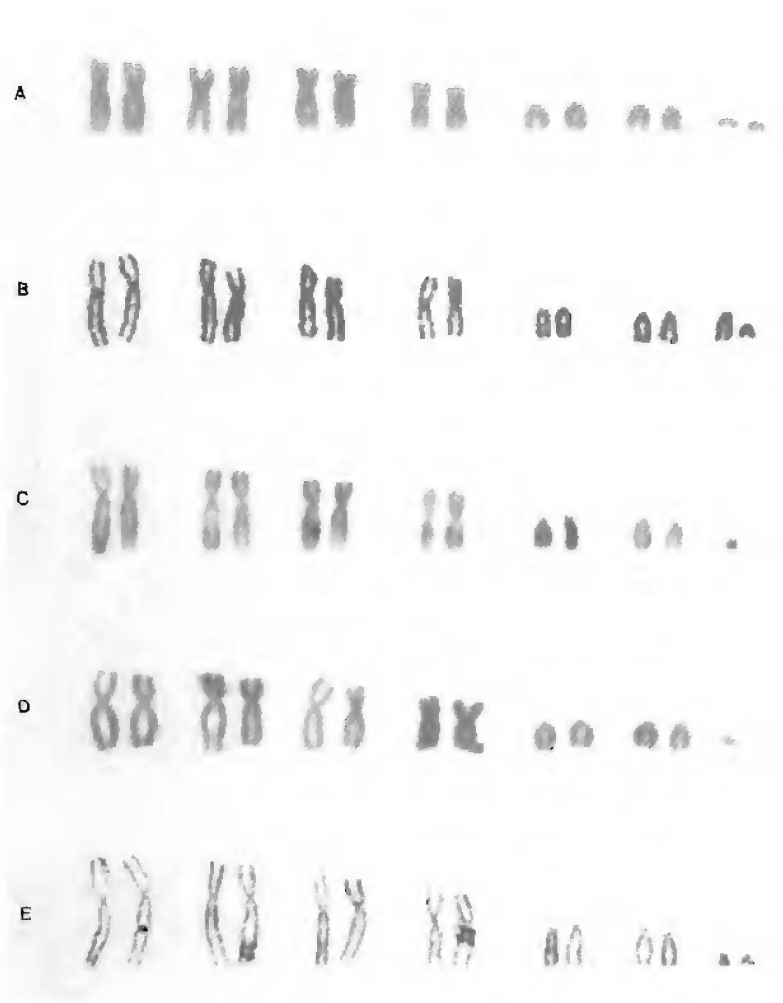

Fig 2. Standard karyotypes of Bolivian marsupials: A) *Micoureus cinereus* (NK 25713, female); B) *M. constantiae* (MSB 57001, male); C) *Thylamys elegans* (NK 23952, male); D) *T. pallidior* (MSB 57003, male); E) *T. pusillus* (NK 25138, female). Localities are given in Materials and Methods.

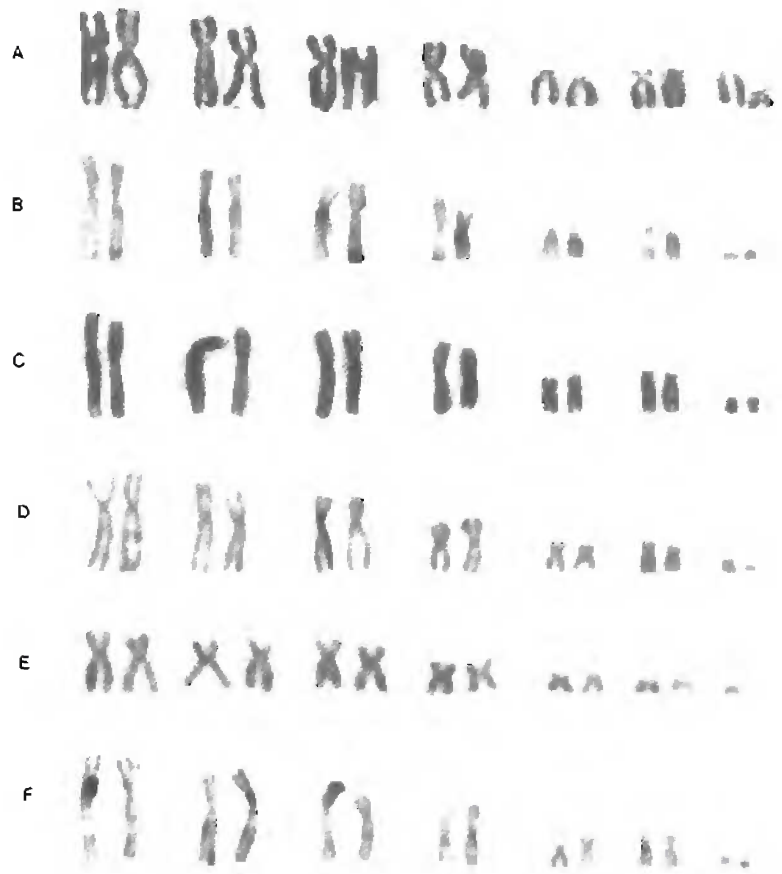

Fig. 3. Standard karyotypes of Bolivian marsupials: A) *Caluromys lanatus* (NK 13953, male); B) *Metachirus nudicaudatus* (MSB 68332, female); C) *Gracilinanus agilis* (NK 23095, female); D) *Marmosops dorothea* (MSB 68334, male); E) *M. noctivagus* (MSB 68333, male); F) *M. parvidens* (NK 25679, female). Localities are given in Materials and Methods.

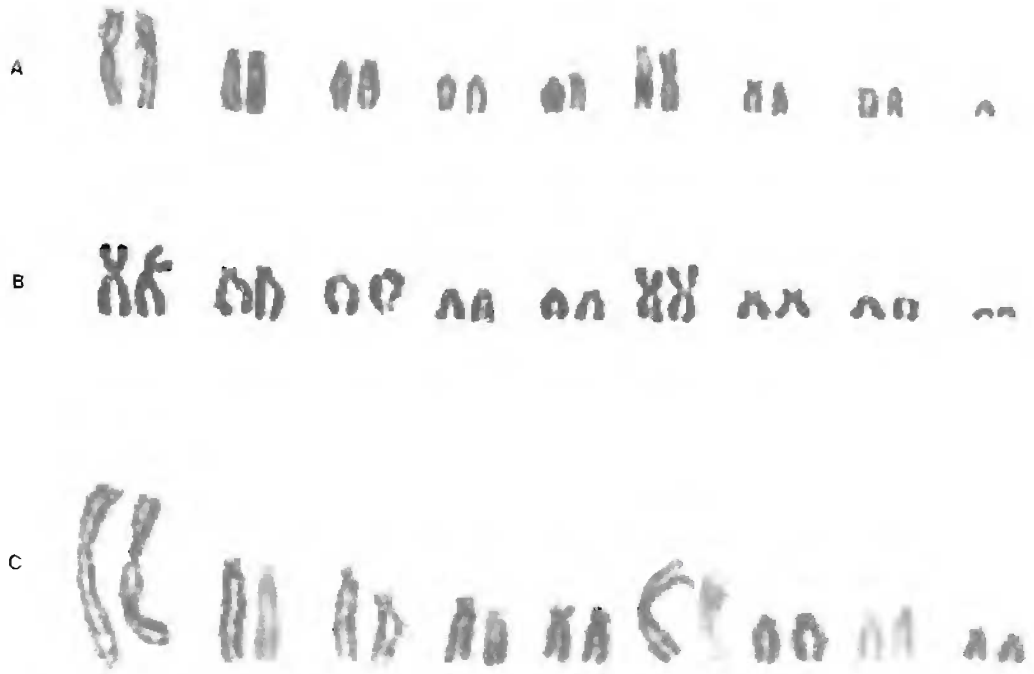

Fig. 4 Standard karyotypes of Bolivian marsupials A) *Monodelphis brevicaudata* (MSB 57005, male), B) *M. domestica* (MSB 55851, female); C) *M. kunsi* (NK23374, female). Localities are given in Materials and Methods

Fig 5 Standard karyotypes of Bolivian marsupials A) *Chironectes minimus* (NK 25586, male), B) *Didelphis albiventris* (NK 14628, female), C) *D. marsupialis* (NK 25299, male), D) *Lutreolina crassicaudata* (NK 23731, male), E) *Philander opossum* (MSB 57007, female). Localities are given in Materials and Methods.

Table 1. Standard chromosomal data for 19 species of Bolivian didelphid marsupials. Abbreviations are 2N (diploid number), FN (number of autosomal arms), SM (submetacentric), A (acrocentric), X (X chromosome), and Y (Y chromosome).

Species	2N	FN	M	SM	A	X	Y
Caluromys lanatus	14	22	2	8	2	A	M
Metachirus nudicaudatus	14	20	2	6	4	A	–
Gracilinanus agilis	14	24	2	10	–	SM	SM
Marmosops dorothea	14	24	2	10	–	M	A
Marmosops noctivagus	14	24	2	10	–	SM	–
Marmosops parvidens	14	24	2	10	–	SM	–
Micoureus cinereus	14	20	2	6	4	A	–
Micoureus constantiae	14	20	2	6	4	A	A
Thylamys elegans	14	20	2	6	4	A	–
Thylamys pallidior	14	20	2	6	4	A	–
Thylamys pusillus	14	20	2	6	4	SM	–
Monodelphis brevicaudata	18	22	2	4	10	A	A
Monodelphis domestica	18	24	2	6	8	A	A
Monodelphis kunsi	18	30	2	12	2	SM	SM
Chironectes minimus	22	20	–	–	20	A	–
Didelphis albiventris	22	20	–	–	20	A	A
Lutreolina crassicaudata	22	20	–	–	20	M	A
Philander opossum	22	20	–	–	20	A	A

chromosome in mouse opossums is acrocentric, but in *T. elegans*, *T. pallidior*, and *M. noctivagus*, it is indistinguishable (Figs. 2c, 2d, and 3e). In *Micoureus constantiae* the Y chromosome is a very distinguishable small acrocentric (Fig. 2b). The X chromosome of *Caluromys* is a medium sized acrocentric, and the Y chromosome a small metacentric. The X chromosomes in *Metachirus* are small acrocentrics (Fig. 3b).

2n = 18 karyotype

This karyotype is only found in *Monodelphis*. The autosomic complements of *M. brevicaudata*, and *M. domestica* (Figs. 4a and 4b) are more similar to each other than either is to *M. kunsi* (Fig. 4c). The three species have the same number of metacentrics (2), however, *M. kunsi* (FN = 30) has eight more bi-armed elements than *M. brevicaudata* (FN = 22), and six more if contrasted to *M. domestica* (FN = 24; Table 1). The X chromosome in *M. brevicaudata* and *M. domestica* is acrocentric, but in *M. kunsi* this element is submetacentric (Fig. 4c). The Y chromosome of *M. brevicaudata* is a "dot-like" acrocentric (Fig. 4a).

2n = 22 karyotype

The autosomic complements of *Didelphis albiventris*, *D. marsupialis*, *Chironectes minimus*, *Philander opossum*, and *Lutreolina crassicaudata* (FN = 20) appear identical, with all of them composed of acrocentrics (Fig. 5). The only difference detected among these species is restricted to the X chromosome of *L. crassicaudata*, which is a small metacentric structure (Fig. 5d), whereas in other taxa it is a small acrocentric. The Y chromosome in *Chironectes* is indistinguishable (Fig. 5a), like in *Thylamys* and *M. noctivagus*.

DISCUSSION

Some authors have suggested that differences in rates of chromosomal evolution are due to differences in effective population size and thus driven by genetic drift (Bush, 1975). Others have emphasized the adaptive value of chromosomal change, and the potential impact that these changes might have for the organism's adaptation to its environment (Nevo, 1978; Bickham and Baker, 1979; John, 1981). However, the high degree of homogeneity in the diploid and fundamental number of opossums contrasts sharply with the extensive heterogeneity of habitats on which these marsupial species occur. For example, the three species of *Thylamys* documented here, occur in remarkably different habitats, but their autosomal complement is almost identical; the aquatic opossum *Chironectes* also has an identical autosomal pattern if compared with the sylvan-pastoral *Didelphis*. This pattern of chromosomal homogeneity ia also a characteristic of other marsupial taxa (Hayman, 1990). For example, 41 species of the Australasian family Dasyuridae, have the 2n = 14 karyotype, and the chromosome morphology among karyotypes is extremely similar (Hayman, 1990). Fifteen of the 47 species of mouse opossums that occur in the Neotropical Region, also have the the 2n = 14 karyotype (Reig *et al.*, 1977; Hayman, 1990; Palma, 1995). The only known deviation from the 2n = 14 pattern for a mouse opossum was the 2n = 22 condition reported for *Marmosa canescens* from western Mexico (Engstrom and Gardner, 1988). Furthermore, South American taxa *Caenolestes*, *Lestoros*, and *Rhyncholestes* (Caenolestidae), and *Dromiciops* (Microbiotheriidae), have species with a diploid number of 14 (Gallardo and Patterson, 1987; Reig *et al.*, 1987). Additionally, it has been shown using G-banding patterns that 2n = 14 karyotypes between Australasian and American marsupials have a high degree of linkage conservarism (Rofe and Hayman, 1985).

The 2n = 22 karyotype is also highly homogeneous within American marsupials. The only difference detected among the species reported in this paper is the metacentric X chromosome of *Lutreolina*. This diploid number is also found in Australasian marsupials of the families Macropodidae and Phalangeridae. However, considerable structural differences exist between chromosomes of these and New World taxa (Hayman, 1990).

The 2n = 14 karyotype has been considered the ancestral metatherian cytotype from which other marsupial karyotypes evolved (Reig et al., 1987; Hayman, 1990). This hypothesis is based on two facts: 1) widely distributed marsupials with identical diploid numbers (2n = 14) and similar chromosomal morphology, and 2) similar G-band patterns in the autosomic complement of Australasian and American forms (Rofe and Hayman, 1985). These data support the hypothesis that fission rather than fussion events account for the primary type of numerical change in these taxa (Hayman, *et al.*, 1987; Reig *et al.*, 1987; Hayman, 1990). The 2n = 18 karyotype found in *Monodelphis* is considered either an intermediate didelphoid karyotype in the evolution of American marsupials from a primitive condition of 2n = 14 (Reig and Bianchi, 1970; Reig *et al.*, 1977), or a separate derivation from 2n = 14 (Reig *et al.*, 1987). When a 2n = 14 karyotype is compared with that of a *Monodelphis*, the karyotype of the latter can be derived from the 2n = 14 cytotype by centromeric fission of two pairs of large metacentrics.

An interesting characteristic of the karyotype of the males of some of the species examined by us is the "missing" Y chromosome. This condition was observed in at least some species in the genera *Thylamys*, *Marmosops*, and *Chironectes* (Figs. 2, 3 and 5) and since karyotypes of males were not available for some species examined in this study, it is possible that this condition may be more widespread than reported here. The apparent lack of an obvious Y chromosome is difficult to determine with our methods. It is possible that the Y has been translocated to another chromosome or this condition may be another example of chromosome mosaicism, i. e. a difference in sex chromosome composition between the germ line and cells of the somatic tissues (Hayman, 1990). Other reports of this type of mosaicism have been made for Australasian marsupials of the families Peramelidae (where one of the X chromosomes is missing in the somatic cells of females), and in *Petauroides volans* (Petauridae), where the Y chromosome is missing from the majority of cells obtained from bone marrow (Murray *et al.*, 1979; Hayman, 1990). All of the cells examined by us, however, showed a homogeneous condition for this trait and no case was observed where the Y chromosome was present in some cells of an individual but absent from others.

Another, American marsupial in which the same "missing" Y condition may occur is the microbiotheriid *Dromiciops australis* (Gallardo and Patterson, 1987). These authors found an apparently identical condition in bone marrow cells of the microbiotheriid marsupial *Dromiciops*. Because of this, Gallardo and Patterson hypothesized that *Dromiciops* was more closely related to Australasian than to American marsupials, supporting Szalay's (1982) contention that *Dromiciops* and Australasian metatherians constitute the cohort Australidelphia. Data from our analyses suggest that this phenomenon may be found not only in *Dromiciops* and Australasian marsupials, but in other American marsupials as well. If true, this scenario fits a typical case of parallelism or represents a plesiomorphic condition in the evolution of metatherian sexual chromosomes of both geographic regions. Hence, this character state cannot be utilized as evidence for inferring phylogeny between Australian and American marsupial lineages.

Despite having a wide latitudinal and altitudinal distribution, mouse opossum are remarkably uniform cytogenetically. The *Thylamys* species included in this study are typical examples. *Thylamys elegans* from Bolivia occurs at high elevations in the Andes, and also in the eastern lowlands. It has been proposed that this form is the same species that occurs in the Coastal Desert of Chile and Peru (Cabrera, 1958; Mann, 1978). Karyotypic data are consistent with this hypothesis since the Chilean form has a karyotype indistinguishable from the one reported here (Reig *et al.*, 1972). *Thylamys pallidior* is restricted to the rocky slopes of the Andean Altiplano, at altitudes exceeding 3500 m (Tate, 1933). *Thylamys pusillus* is restricted to the Chaco of Bolivia, and Argentina and Paraguay, and probably the Monte Desert of Argentina (Gardner, 1993). *Micoureus cinereus* occurs at elevations no higher than 1000 m, associated with dense forest and shrubland habitats. *Micoureus constantiae* has a more restricted range, occurring between the Mato Grosso of Brazil, to the eastern Bolivian lowlands (Tate, 1933). *Gracilinanus agilis* in Bolivia has been obtained in forests and bushy areas, in sympatry with *M. cinereus*. This report of *Marmosops parvidens* in Bolivia, represents the first record for this country. It is associated with moist habitats of the Amazon Basin (Eisenberg, 1989; Emmons and Feer, 1990). The Bolivian record

extends the known range of this species into subtropical moist forests. *Marmosops noctivagus* is also restricted to moist forests of the Amazon Basin and subtropical habitats, while *M. dorothea* inhabits montane humid forests (Emmons and Feer, 1990). *Metachirus nudicaudatus* was trapped in forested habitats, at low elevations under 1000 m. The Woolly Opossum *Caluromys lanatus* was collected in moist forests of Pando Department.

Monodelphis kunsi is known only from Bolivia (Anderson, 1982) in forested and bushy areas at middle elevations. *Monodelphis brevicaudata* occurs in disturbed and secondary forests. Finally, *M. domestica* which is primarily found in xeric habitats (Redford and Eisenberg, 1992), occurs in forested , bushy and grassy areas of Bolivia.

Among the larger South American opossums, *Chironectes minimus* is unique in its aquatic mode of life. In Bolivia, the species is known to inhabit low elevational rivers under 1000 m (Salazar et al., in review). *Lutreolina crassicaudata* is restricted to dense moist habitats, and in Bolivia has been recorded in the Pando, and Beni, and Santa Cruz Departments. *Didelphis albiventris* has a wide distribution in South America but is most common in cerrados, brushland and grassy areas (Gardner, 1973). In Bolivia it is known from middle elevations (1500 m). *Didelphis marsupialis*, is more restricted to moist forest, and has a distribution centered in the Amazon basin (Emmons and Feer, 1990).

Marsupial radiation has occurred within a conservative karyotypic framework, for both American and Australasian taxa. In this sense, karyotypic stability of marsupials does not fit the predictions of the canalization model (Bickham and Baker, 1979). For example, sigmodontine rodents are the ecological equivalents to mouse opossums, and contemporaneous to marmosines in the fossil record of South America (Reig *et al.*, 1987). Both groups have a great array of taxa, radiated to different habitats, and date from the Plio-Pleistocene of South America (Reig *et al.*, 1985; Webb, 1991). One of the predictions of the canalization model states that "the longer a taxon has occupied an adaptive zone, the more probable it will be that the taxon will have achieved karyotypic stability" (Bickham and Baker, 1979:81). The biogeographic history has established a similar scenario for both groups, however, mouse opossums remained karyotypically stable, whereas sigmodontine rodents show one of the greatest karyotypic

differentiation known for mammals (Gardner and Patton, 1976; Pearson and Patton, 1976; Reig, 1989). Another aspect of the karyotypic evolution of marsupials that contrasts with the Bickham and Baker model, is the non-Robertsonian (e.g., inversion) differences found in marsupials. Contrary to canalization expectations, there are fixed non-Robertsonian differences between genera within the Australasian families dasyuridae and Burramyidae, and between Didelphidae and Australasian families (Sites and Moritz, 1987).

The nature of the constraints that restricted the chromosomal change in marsupials is not known. Reig *et al.* (1987) suggested that karyotypic stability in marsupials was based on a dichotomy that chromosomal evolution took in the radiation of mammals. Assuming that metatherians and eutherians evolved from a common ancestor about 100 million years ago (Hope *et al.*, 1990), chromosomal evolution in eutherians, probably linked to selection for new regulatory mechanisms (Wilson *et al.*, 1974). It is interesting that chromosomal evolution in marsupials appears to be from low to high diploid number, whereas the opposite case is true for most other mammalian groups. A similar trend appears to be present in moles of the family Talpidae (Yates and Modre, 1990) which is also conservative in terms of chromosomal evolution. An understanding of the role of chromosomal change in speciation may be enhanced by a better knowledge of chromosomal change in didelphid marsupials.

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